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Prescribed burning is the major viable option that land managers have for reducing hazardous fuels and ensuring the regeneration of fire-dependent species in a cost-effective manner in Pine Barren ecosystems. Fuels management activities are directly linked to carbon (C) storage and rates of C sequestration by forests. To evaluate the effects of prescribed burning on forest C dynamics, we quantified consumption and accumulation of the forest floor and understory vegetation and measured net CO_2 exchange in upland forest stands in the New Jersey Pinelands burned with prescribed fires. Prescribed fires released an average of 470 ± 137 g C m^{-2} from the litter layer and understory, equivalent to approximately 2–3 yr of sequestered C in undisturbed upland forests. Canopy and understory foliage averaged 85% of preburn periods, and CO_2 uptake at near-full sunlight conditions averaged 79% of preburn levels during the following growing season. On an annual basis, stands lost C during the year of the burn, but released C was recovered within 2–3 yr. Field measurements and model simulations suggest that continued prescribed burning in upland fire-dependent pine-dominated stands would have little appreciable effect on long-term forest C dynamics at the landscape scale.

KEYWORDS prescribed fire, carbon sequestration, net CO_2 exchange, pitch pine, Pine Barrens, New Jersey Pinelands

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INTRODUCTION

All hazardous fuels management activities affect carbon (C) storage and rates of C sequestration by forests to some degree. Thus, it is important to understand how prescribed fires and mechanical fuel management practices potentially impact short- and long-term forest C dynamics. The litter layer and understory vegetation are consumed during prescribed fires or redistributed during thinning treatments (Stephens et al., 2012). Following fuel-reduction treatments, net carbon dioxide exchange with the atmosphere (NEE_c) is affected because consumption or loss of leaf area and biomass of respiring tissue reduces rates of C assimilation and ecosystem respiration (Amiro et al., 2010). Fuel-reduction treatments can also affect the turnover of C and nutrients by altering forest floor and soil pools (Gray & Dighton, 2006; Neill, Patterson, & Crary, 2007; Boerner, Huang, & Hart, 2009; Williams, Hallgren, & Wilson, 2012). Long-term rates of C sequestration can be affected by changes in stand age and composition caused by repeated prescribed fires, wildfires, or fire suppression, potentially altering C storage in tree boles, forest floor, and soil (Little, 1979; Scheller, Van Tuyl, Clark, Hom, & La Puma, 2011; La Puma, Lathrop, & Keuler, 2013).

Carbon dioxide (CO_2) is now considered a pollutant as a result of the Endangerment Finding issued by the Environmental Protection Agency (EPA; 549 U.S. 497, 2007). The EPA may require that land managers quantify and report CO_2 emissions from forest operations in the near future, including hazardous fuel-reduction treatments, as part of a modification to the Clean Air Act. A better understanding of how fuel-reduction treatments affect forest C dynamics can help guide management practices to achieve maximum effectiveness, which can be influenced by a suite of factors including initial fuel mass and structure, fuel moisture content, meteorological conditions, ignition timing and firing patterns during prescribed burns, and seasonal timing of management activities. Accurately quantifying C dynamics associated with fuel-reduction treatments also facilitates an evaluation of the trade-offs between treatments and unmitigated wildfires, which typically have larger emissions and longer recovery times (Mitchell, Harmon, & O'Connell, 2009; Dore et al., 2010; Wiedinmyer & Hurteau, 2010; Restaino & Peterson, 2013).

Calculating CO_2 emissions during fuel-reduction treatments that employ prescribed burning requires an accurate estimate of the amount of fuel consumed, either by directly quantifying preburn and postburn fuel mass, or more commonly by using local meteorological data, the appropriate fuel models, and fire behavior simulators to estimate consumption (e.g., CONSUME, FOFEM; Scott & Burgan, 2005; Ottmar, Anderson, DeHerrera, & Reinhardt, 2006; French et al., 2011; Ottmar, 2013). Recent research has focused on measuring and modeling fuel mass and consumption during prescribed fires in Pine Barren ecosystems of the northeastern United States (Wright, Ottmar, & Vihnanek, 2007; Clark et al., 2009; Clark, Skowronski, Gallagher, Heilman, & Hom, 2010b; Clark, Skowronski, Renninger, & Scheller, 2014b), including the use of Light Detection and Ranging Systems (LiDAR) to detect the effects of single and repeated prescribed burns on understory and canopy fuels (Skowronski, Clark, Nelson, Hom, & Patterson, 2007; Skowronski, Clark, Duveneck, & Hom, 2011; Clark et al., 2009; Clark et al., 2013).

While significant progress has been made in estimating C emissions during fuel-reduction treatments in Pine Barren ecosystems of the northeastern United States, less information is available on short- and long-term forest C dynamics following fuel-reduction treatments. Remotely sensed and Geographical Information System (GIS) information detailing the history of prescribed fires and thinning treatments are available for many areas, and overall changes in forest composition and structure with fire and fire suppression are well-documented (Little & Somes, 1961; Little, 1979; La Puma et al., 2013; Bried, Patterson, & Gifford, 2014). However, data are limited on rates of recovery of vegetation and the forest floor or factors controlling NEE_c following fuel-reduction treatments (Burns, 1952; Little, 1979; Neill et al., 2007; Clark et al., 2009; Clark et al., 2014b). In other conifer-dominated ecosystems, the impacts of wildfires on stand to landscape scale C dynamics have been quantified using biometric plots (Campbell, Donato, Azuma, & Law, 2007; Campbell, Harmon, & Mitchell, 2011) and eddy covariance techniques (Amiro et al., 2010; Dore et al., 2010; Mkhabela et al., 2009) and simulated using process-based models (Thornton et al., 2002; French et al., 2011). In a number of these investigations, C dynamics following severe wildfires were studied, and annual NEE_c was still negative $\geq$ 10 yr after the fire (Mkhabela et al., 2009; Amiro et al., 2010; Dore et al., 2010). However, these results are not likely to be directly comparable to the longer term effects of prescribed fires, which are usually much less severe and are typically not conducted during extreme fire weather conditions.

The current study addresses how prescribed burning affects short- and long-term forest C dynamics in fire-dependent upland forest communities in the New Jersey Pinelands National Reserve (hereafter "Pinelands"). Our major objective was to assess whether prescribed burning in upland forest units managed by the New Jersey Forest Fire Service (NJFFS) in the Pinelands resulted in a net gain or loss of C over typical fire-free rotation intervals of 5 to 8 yr. Our specific objectives were to: (a) characterize forest floor and understory biomass in prescribed burn units managed by the NJFFS to determine variation with time and among the three major upland forest communities in the Pinelands, (b) estimate consumption of the forest floor and understory during prescribed burns to develop equations for predicting consumption as a function of initial values, (c) quantify the major biotic and environmental controls over C dynamics following selected prescribed burns using a combination of biometric and eddy covariance measurements, and (d) develop predictive equations for the accumulation of the forest floor and understory vegetation following prescribed fires as a function of time since last fire. We then integrated fuel consumption measurements, information on net CO_2 exchange, and fuel accumulation data collected during 5- to 8-yr fire-free intervals following treatments to estimate the effects of prescribed fires on C dynamics in prescribed burn units in selected upland forest stands.

METHODS AND MATERIALS

Study Area

Research sites were located in Burlington and Ocean Counties in the Pinelands National Reserve in southern New Jersey, USA. The Pinelands encompass approximately 445,000 ha of upland and wetland forest and represents the largest continuous forested landscape on the Northeastern U.S. Coastal Plain. The climate is cool temperate, with mean monthly temperatures of 0.3 and 23.8°C in January and June, respectively (1930–2004; State Climatologist of NJ). Mean annual precipitation is 1,123 ± 182 mm (mean ± *SD*; Clark, Skowronski, Gallagher, Renninger, & Schäfer, 2012). Soils are derived from the Cohansey and Kirkwood Formations (Lakewood and Lakehurst series) and are sandy, coarse-grained, and have low nutrients status and cation exchange capacity (Tedrow, 1986). Upland forests occupy 62% of the forested areas in the Pinelands, and many stands are closed-canopy and nearly even-aged with an average age of approximately 60–90 yr. Upland forests are dominated by three major communities: (a) oak-pine, consisting of chestnut oak (*Quercus prinus* L.), white oak (*Q. alba* L.), scarlet oak (*Q. coccinea* Muenchh.), black oak (*Q. velutina* Lam.), pitch pine (*Pinus rigida* Mill.), and shortleaf pine (*P. echinata* Mill.); (b) pine-oak, consisting of predominately pitch pine with scattered mixed oaks in the overstory; and (c) pine-scrub oak, dominated by pitch pine with scrub oaks (*Q. ilicifolia* Wang., *Q. marlandica* Muench.) in the understory (McCormick & Jones, 1973; Lathrop & Kaplan, 2004; Skowronski et al., 2007). Understory vegetation in all three forest communities consists of ericaceous shrubs—primarily huckleberry (*Gaylussacia bacata* [Wang.] K. Koch, *G. frondosa* [L.] Torr. & A. Gray ex Torr.), blueberry (*Vaccinium* spp.), and scrub oaks. Sedges, mosses, and lichens also are present.

Many upland forest stands in the Pinelands have regenerated naturally following cessation of logging and charcoaling activities in the late 1800s. Following this period of intensive forest management, large wildfires totaling 40,000+ ha per year were common in regenerating forests prior to modern fire suppression practices starting in the 1940s (Forman & Boerner, 1981; La Puma et al., 2013). Limited use of prescribed fire as a tool to reduce wildfire risk was initiated in the late 1920s in the Pinelands, and it has been used by the NJFFS since 1948 (Little & Moore, 1949; Little & Somes, 1961; Clark, Skowronski, & Gallagher, 2014a). Reliable spatial data for wildfire areas > 45 ha and their dates exist back to 1925, and data for prescribed burn units and dates exist back to the 1960s (NJFFS, unpublished data; Clark et al., 2009; La Puma et al., 2013). Currently, the NJFFS and federal wildland fire managers conduct an average of 129 ± 31 prescribed burns on 4,650 ± 2,000 ha per year (mean ± *SD*; National Interagency Fire Center [NIFC], 2013). Prescribed burns are conducted from January through March within a relatively narrow window of appropriate meteorological conditions, with air temperature typically not exceeding 16°C and with relative humidity above 40%.

Fuel Biomass and Consumption Measurements

We sampled the forest floor in 32 prescribed burn units managed by the NJJFS in the Pinelands, distributed among the three upland forest communities ($n = 5$ units in oak-pine stands, 190 ± 66 ha in size; $n = 14$ units in pine-oak stands, 251 ± 110 ha in size; $n = 13$ units in pine-scrub oak stands, 111 ± 113 ha in size; mean ± *SD*). Time since last prescribed burn or wildfire ranged from 2 yr in a fuel control strip to approximately 45 yr at two stands that had not burned since 1962 (prescribed burn) or 1963 (wildfire in April 1963). Mass of fine material (leaves, needles) and woody 1-hr (< 0.6 cm diameter), 10-hr (0.6 to < 2.5 cm diameter) and 100-hr (2.5 to < 7.6 cm diameter) fuels on the forest floor were sampled in 10 to 30 1-m^2 plots distributed in random locations in each burn unit. We sampled only fuels in the litter layer (L horizon) of the forest floor, because field observations indicated that prescribed fires rarely burned into the more highly decomposed organic layer (O horizon). Samples were sorted, and any residual sand and organic material from the O horizon was separated by sequentially sifting samples using 10 mm and then 2 mm mesh screens, and then discarded. Samples were then dried at 70°C and weighed. Understory shrubs and scrub oaks < 2 m height were destructively sampled at 15 of the burn units sampled for forest floor mass using the same 1-m^2 plots. Aboveground stems that occurred in each 1-m^2 plot were harvested, separated into live and dead foliage and live and dead stems by 1-, 10-, and 100-hr size classes, and then dried and weighed.

At 28 of the burn units where we sampled the forest floor, the NJFFS or federal wildland fire managers conducted prescribed burns, and then postburn forest floor biomass was sampled within 2 weeks of each fire. At each burn unit, we sampled remaining fine and woody 1-, 10-, and 100-hr fuels on the forest floor using 10 to 30 1-m^2 plots distributed at random locations. Samples were processed in the same manner as the preburn samples. Consumption of understory vegetation during prescribed burns was estimated in 13 of the burn units sampled for preburn understory biomass within 2 weeks of each fire by clipping all remaining standing stem material in the same 1-m^2 plots sampled for postburn forest floor material, sorting them by size class, and then drying and weighing stems.

Subsamples of oak foliage, pine needles and wood on the forest floor and shrub and understory oak stems were analyzed for C content using a C/N analyzer (Leco Carbon/Nitrogen Determinator 200-288, Leco, Inc., St. Joseph, MI, USA) and mass loss on ignition at 550°C. Biomass data were then converted to C content by multiplying by the appropriate conversion factor.

Biometric Measurements and Net CO_2 Exchange

We used repeated biometric measurements prefire and postfire and eddy covariance to measure NEE_c to quantify stand C dynamics over a 10-yr period at an intensively-studied 143 ha pitch pine-scrub oak stand in Greenwood Wildlife Management Area in the Pinelands (Skowronski et al., 2007; Clark, Skowronski, & Hom, 2010a; Clark et al., 2012). We measured biometric variables for 4 yr (2004–2007) and NEE_c for 3 yr (2005–2007) to establish preburn baseline data, and then the NJFFS conducted prescribed burns at the stand on March 22, 2008 and March 15, 2013. Tree biomass, litterfall, and shrub biomass were measured from 2004 to 2013 in or near five circular, 201 m^2 forest census plots located at random distances and directions within a 150 m radius of an eddy covariance tower, described below. Annual measurements of tree diameter at breast height (dbh; 1.37 m) and tree height were conducted for all stems $\geq$ 5.0 cm dbh in each plot, and tree and foliar biomass were estimated from published allometric relationships (Whittaker & Woodwell 1968, Skowronski et al., 2007, Clark et al., 2013). Fine litterfall was collected approximately monthly when present from two 0.42 m^2 wire mesh traps adjacent to each tree census plot ($n = 10$ traps in total). Litterfall was separated into leaves, needles, stems, and reproductive material of trees and shrubs and of sedges and herbs, and then dried at 70°C and weighed. Foliage and aboveground stem biomass of understory shrubs and scrub oaks (< 2 m tall) were estimated by harvesting 10 to 20 clip plots (1.0 m^2) in the vicinity of the tree census plots every year during the time of peak biomass in mid-summer (July or August), immediately prefire and postfire in 2008 and 2013, and in early June of 2008 and 2013. Understory vegetation samples were separated into leaves, stems, and reproductive material, and then dried at 70°C and weighed. Specific leaf area (SLA; m^2 g dry weight^{-1}) for each major species was measured with a leaf area meter (LI-3000a, Li-Cor Inc., Lincoln, NE, USA) and a conveyer belt (LI-3050c, Li-Cor Inc.) using fresh leaf, needle, or litter samples, which were then dried at 70°C and weighed. Maximum annual canopy leaf area index (LAI, m^2 m^{-2} ground area) was estimated for each species by multiplying litterfall mass by the appropriate SLA value and then summing results for all species. Projected leaf area of pine needle fascicles was multiplied by π to calculate an all-sided LAI (Gholz, Linder, & McMurtrie, 1994). Understory LAI was estimated by multiplying foliage mass from clip plots by the corresponding SLA values.

Eddy covariance and meteorological measurements were made from a single 15.5 m tower located approximately 200 m east of the Cedar Bridge fire tower in the 143 ha intensively studied pine-scrub oak stand. Additional understory meteorological measurements were made from a 3 m tower located within 25 m of the above-canopy tower. Meteorological and eddy covariance measurements were made on a near-continuous basis from early 2005 until present. Details of the eddy covariance and meteorological instrumentation, sample processing, and gap filling procedures appear in Clark, Skowronski, and Hom (2010a) and Clark et al. (2012). All eddy covariance and meteorological data are available on the Ameriflux website (US-Ced; http://ameriflux.lbl.gov).

Accumulation of Fuels Following Prescribed Fires

Two sources of data were used to estimate accumulation rates of the litter layer and understory vegetation following prescribed burns: (a) the chronosequence based on time since last fire of the 32 (15 for understory vegetation) prescribed burn units sampled for preburn and postburn fuel characteristics described above, and (b) forest floor and understory biomass samples collected at the intensively studied pine-scrub oak stand described above and at a second flux tower site located in a pine-oak stand on the Department of Defense McGuire-Dix-Lakehurst Base that was burned in 2000 and 2006 (US-Dix; described in Clark, Skowronski, & Hom, 2010a; Clark et al., 2012). Time since last fire along the chronosequence ranged from 2 to 45 yr, the latter in a pine-scrub oak stand that had not burned since a large wildfire in 1963. Maximum time since last fire at the intensively studied pine-scrub oak stand was 14 yr. Data from both sources were pooled to calculate equations to predict accumulation of the forest floor or understory vegetation as a function of time since last fire.

Forest Carbon Dynamics During Prescribed Fire Intervals

We integrated initial forest floor and understory vegetation biomass measurements, consumption data during prescribed burns, information on preburn and postburn NEE_c, and accumulation data for the forest floor and understory vegetation following burns to calculate average rates of net C accumulation spanning prescribed fires and over the 5- to 8-yr fire-free intervals in representative burn units in upland forest stands. We used these analyses to evaluate whether typical rotation intervals employed by the NJFFS in management units resulted in a net gain or loss of C.

Statistical Analyses

ANOVAs were used to compare biomass and consumption of forest floor and understory vegetation among the three upland forest communities (SYSTAT 12, SYSTAT Software, Inc., San Jose, CA, USA). Tukey's honestly significant differences (HSD) were used to test contrasts when ANOVA analyses detected significant differences among forest communities. Parameters and statistics for linear relationships between initial forest floor mass and consumption or between initial understory biomass and remaining stem mass following prescribed fires were calculated using SigmaPlot 10 curve fitting software (SYSTAT, Inc.). Linear and nonlinear functions to estimate accumulation of the forest floor or understory vegetation as a function of time since last fire were also calculated using SigmaPlot curve fitting software.

RESULTS

Forest Floor and Understory Fuels

Initial fine litter and wood (1-hr and 10-hr size classes) on the forest floor averaged 1,264 ± 334 g m^{-2} for the 32 prescribed burn units in the three upland forest communities sampled (mean ± *SD* is used throughout; Figure 1). Forest floor biomass increased with time since last fire, with values ranging from 530 ± 210 g m^{-2} in a fuel break that was burned at 2- to 3-yr intervals to 2,338 ± 600 g m^{-2} in a pine-scrub oak stand that had not burned since a large wildfire in 1963. Fine litter was greater in pine-scrub oak stands than in oak-dominated stands (ANOVA, $F_{2,29} = 7.0$, $p < .01$; HSD $p < .05$), but woody 1 + 10-hr fuels were similar among forest communities ($F_{2,29} = 2.7$, $p > .09$). Fine litter and woody 1 + 10-hr fuels together were also significantly different among forest types (ANOVA, $F_{2,29} = 8.3$, $p < .01$), with pine-scrub oak stands having greater forest floor biomass than oak-pine and pine-oak stands (HSD $p < .05$; Figure 1). Live shrub and scrub oak biomass was 474 ± 264 g m^{-2} , and dead shrub and oak stem biomass averaged 130 ± 212 g m^{-2} in the 15 prescribed burn units sampled for understory vegetation. Live + dead stems of shrubs and scrub oaks also increased with time since last fire; maximum live + dead stem biomass averaged 1,174 ± 398 g m^{-2} in a pine-scrub oak stand that had not burned since 1962. Live + dead stem biomass of shrubs and scrub oaks was greater in pine-oak and pine-scrub oak stands than in oak-pine stands ($F_{2,12} = 4.19$, $p < .05$).

Postburn litter and 1 + 10-hr wood on the forest floor averaged 680 ± 256 g m^{-2}, and estimated consumption of forest floor biomass was 578 ± 274 g m^{-2} at the 28 burn units sampled prefire and postfire (Table 1). Consumption of fine litter represented 50.0 ± 14.9% of preburn values, while

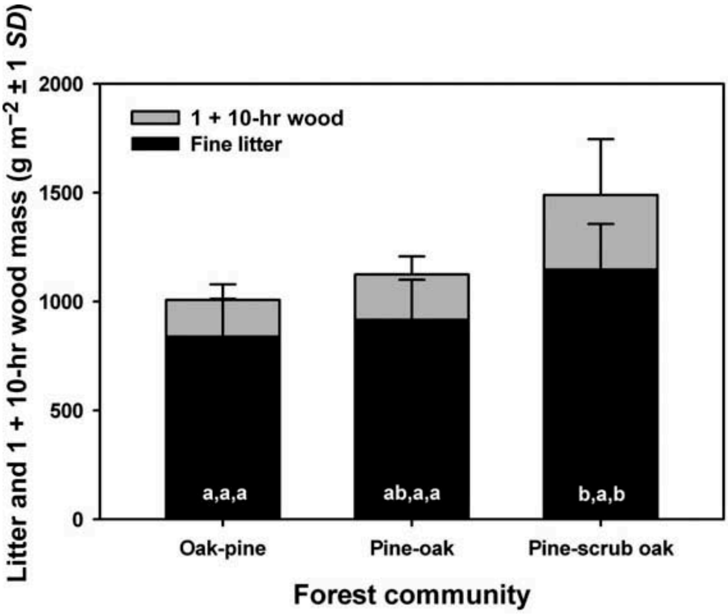

FIGURE 1 Mass of fine and 1-hr and 10-hr woody fuels on the forest floor in 32 upland forest prescribed burn units in the New Jersey Pinelands. Data are mean g m^{-2} ± *SD* of mean values calculated from 10 to 30 1-m^2 plots located at random points throughout each burn unit. Forest communities with different letters are significantly different at $p < .05$ for fine litter, 1 + 10-hr woody fuels, and fine litter and woody fuels combined. Updated data from Clark et al. (2010b).

mean consumption of 1 + 10-hr wood was only 24.5 ± 39.6%. Actual consumption of 1 + 10-hr fuels on the forest floor was likely greater, because some shrub and oak stems likely fell to the forest floor during and immediately following prescribed burn treatments. Greater consumption of fine litter occurred in pitch pine-scrub oak stands compared to oak-pine stands (Table 1; $F_{2,25} = 4.03$, $p < .05$), but consumption of 1 + 10-hr wood was similar among stands. For the 13 prescribed fires where consumption of understory vegetation was estimated, total preburn biomass of live + dead shrubs and scrub oaks averaged 606 ± 363 g m^{-2} and postburn mass was 273 ± 185 g m^{-2} (Table 1).

Consumption of litter and woody fuels had significant linear relationships with initial fuel loading, which explained 70% of the variability in fine litter consumption and 76% of the variability in 1 + 10-hr wood consumption on the forest floor (Table 2). Consumption of live + dead stems of shrubs and scrub oaks also had a significant linear relationship with initial stem mass, explaining 73% of the variability in stem consumption (most shrubs and understory oaks are deciduous, thus leaf mass was very low during prescribed burns; Table 2).

TABLE 1 Prefire and Postprescribed Fire Forest Floor Mass and Understory Biomass, Estimated Consumption by Fuel Type, and Percent Consumption in the Three Major Upland Forest Communities in the New Jersey Pinelands

Fuel, forest type	n	Size (ha)	Preburn (g m^{-2})	Postburn (g m^{-2})	Consumption (g m^{-2})	% Consumed
Fine litter						
Oak-pine	3	168 ± 61	781 ± 184^{a}	438 ± 113	343 ± 138^{a}	43 ± 14%
Pine-oak	14	270 ± 113	936 ± 204^{ab}	492 ± 106	443 ± 184^{ab}	46 ± 13%
Pine-scrub oak	11	94 ± 61	1107 ± 226^{b}	470 ± 175	637 ± 156^{b}	58 ± 13%
1 + 10-hr wood						
Oak-pine	3	168 ± 61	209 ± 30	138 ± 21	71 ± 50	32 ± 19%
Pine-oak	14	270 ± 113	218 ± 104	134 ± 47	84 ± 89	31 ± 27%
Pine-scrub oak	11	94 ± 61	247 ± 116	165 ± 68	79 ± 153	16 ± 57%
Understory vegetation						
Oak-pine	2	150	169	120	49	29%
Pine-oak	4	180 ± 103	478 ± 167	186 ± 79	371 ± 64	67 ± 12%
Pine-scrub oak	7	95 ± 66	804 ± 360	355 ± 203	449 ± 291	54 ± 24%

Note. n = number of prescribed burn units sampled and size is mean size of prescribed burn units sampled in each forest community. Values are mean g m^{-2} ± 1 *SD*, and different superscripts indicate significant differences at $p < .05$.

TABLE 2 Statistics for the Consumption of Litter and Wood on the Forest Floor, and Shrub and Scrub Oaks in the Understory During Prescribed Burns as a Function of Initial Mass for the Three Major Upland Forest Communities Combined in the Pinelands of New Jersey

Fuel type	n	$\alpha \pm 1$ *SE*	$\beta \pm 1$ *SE*	r^2	F	p
Fine litter		.737 ± 0.091	216.3 ± 91.6	.70	66.2	< .001
1 + 10-hr wood		.925 ± 0.100	128.4 ± 24.5	.76	85.5	< .001
Shrubs and oaks[1]		.635 ± 0.114	84.0 ± 164.4	.73	31.4	< .001

Note. Data were fit to the equation consumption = α * initial mass − β, and values are g m^{-2}.
[1]Includes live and dead stems of 1 + 10-hr size classes.

Biometric Measurements and Net CO_2 Exchange

At the intensively studied pine-scrub oak stand, some crown scorch occurred during the prescribed burn conducted on March 22, 2008, and active, green leaf area immediately following the fire was estimated at only 1.2 ± 0.6 m^2 m^{-2}. Resprouting of foliage from regenerating shrubs and understory oaks starting in early May resulted in the progressive recovery of understory LAI. By the peak of the growing season in 2008, understory LAI reached 1.3 ± 0.3 m^2 m^{-2}, representing > 95% of preburn levels. Expansion of pine needles lagged behind the understory, because the current year cohort of needles had not fully expanded until approximately July 1 (K. Clark, personal observation). Overstory pine LAI then averaged 3.6 ± 0.6 m^2 m^{-2} at the peak of the growing season, representing 71% of preburn maximum LAI. Total LAI had reached 5.0 ± 0.5 m^2 m^{-2} by August 2008, which was approximately 79% of LAI during the growing season of previous years before the burn. During the prescribed burn conducted on March 15, 2013 in the same location, average flame lengths were shorter and little crown scorch occurred, thus overstory LAI was nearly unaffected. Understory LAI had reached 1.6 ± 0.5 m^2 m^{-2} by the peak of the growing season in 2013, and total leaf area was similar to preburn levels.

Following the prescribed burn in 2008 at the intensively studied pine-scrub oak stand, NEE_c at full sunlight conditions during midday (>1,500 μmol photosynthetically active photon flux density [PPFD] m^{-2} s^{-1}) from April to mid-May averaged −3.8 ± 2.2 μmol CO_2 m^{-2} s^{-1}, representing 59% of preburn levels. However, levels averaged only −5.7 ± 1.6 μmol CO_2 m^{-2} s^{-1}, 44% of preburn levels following bud break of deciduous species (Figure 2). With the expansion of new pine foliage starting in early June, NEE_c gradually increased and averaged −10.4 ± 2.7 μmol CO_2 m^{-2} s^{-1} at full sunlight conditions during the June 15th–August 31st period, approximately 70% of preburn levels during the same period (Figure 2). Annual NEE_c at the pine-scrub oak stand during 2008 was only +48 g C m^{-2} yr^{-1}. When consumption of the forest floor and understory during the prescribed burn was included (−442 g C m^{-2}), net C accumulation for 2008 was −396 g C m^{-2} yr^{-1} (Figure 3). Daytime NEE_c during the second growing season in 2009 had recovered to rates characterizing preburn levels, and annual NEE_c was similar to preburn conditions (+169 vs. +183 g C m^{-2} yr^{-1} estimated for 2005 and 2006; Figure 3). Following the less intense prescribed fire in 2013, NEE_c at full sunlight conditions averaged −7.8 ± 2.0 μmol CO_2 m^{-2} s^{-1} immediately after the burn, representing 89% of preburn NEE_c, and −9.9 ± 4.5 μmol CO_2 m^{-2} s^{-1} from mid-May to mid-June, 74% of preburn values during previous years at the same time period. Half-hourly NEE_c then averaged −16.0 ± 3.8 5 μmol CO_2 m^{-2} s^{-1} during full sunlight condition from mid-June to the end of August, representing 99% of preburn values during previous years at the same time period (Figure 2). Annual NEE_c in 2013 was +94 g C m^{-2} yr^{-1}, but consumption of the forest floor and understory was greater than in 2008 (−611 g C m^{-2}). Thus, net C accumulation for 2013 totaled −517 g C m^{-2} (Figure 3).

Accumulation of Fuels Following Prescribed Fires

Accumulation of fine litter on the forest floor estimated as a function of time since last prescribed fire was a linear function of time during the first 14 yr (Figure 4a, Table 3), and averaged 73 ± 18 g m^{-2} yr^{-1}. When a 45-yr time frame was considered (the time since last fire of the "oldest" stands we sampled), fuel accumulation on the forest floor was best approximated as a power function of time since last fire (Table 3). Litter and 1 + 10-hr wood on the forest floor was predicted by the equations (Table 3) to be 1,938 ±

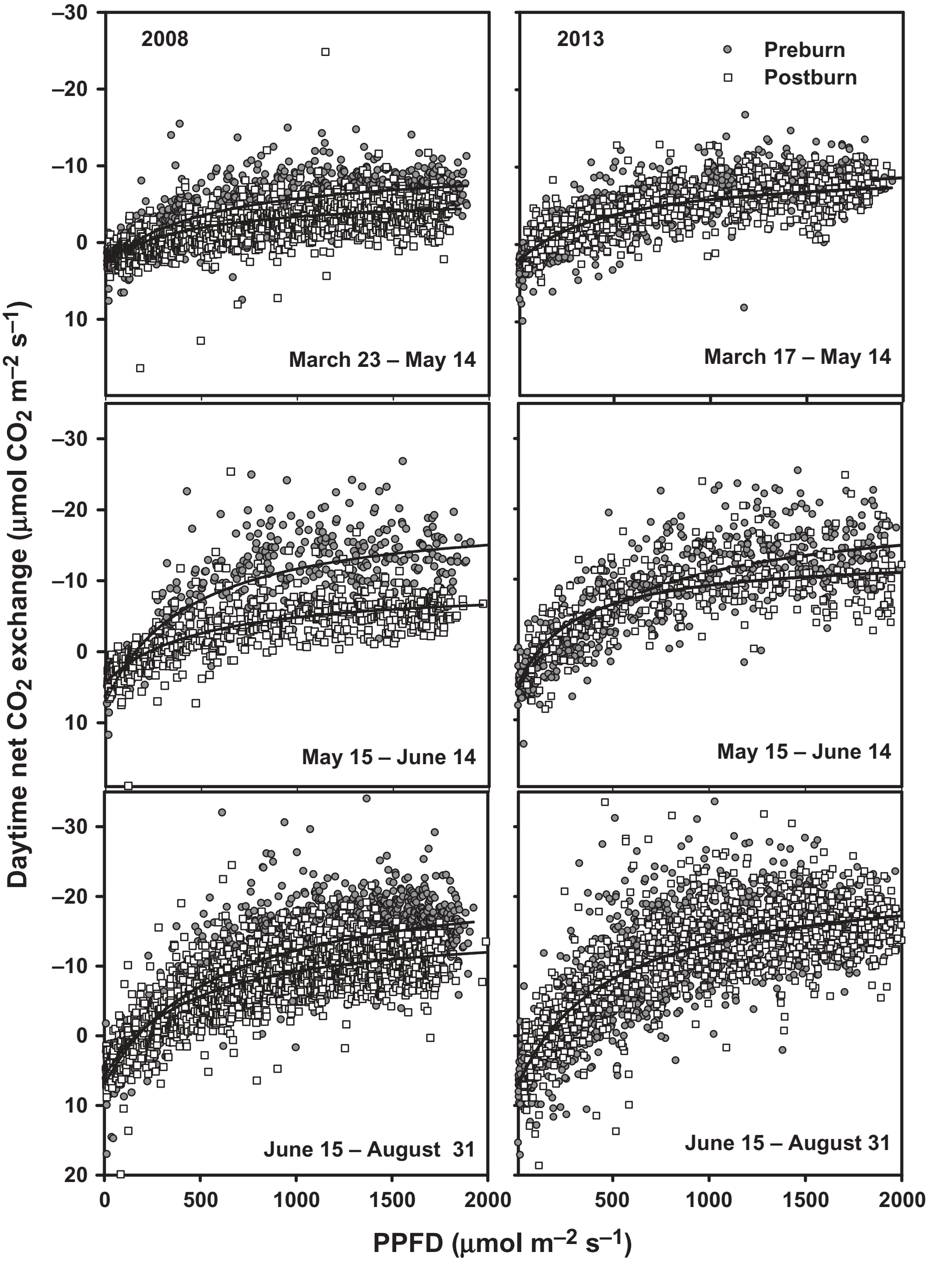

FIGURE 2 Daytime net CO_2 exchange (NEE_c, μmol CO_2 m^{-2} s^{-1}) as a function of photosynthetically active photon flux density (PPFD, μmol m^{-2} s^{-1}) for three time periods within the year prior to and the year following prescribed fires conducted at the intensively studied pitch pine-scrub oak stand in Greenwood Wildlife Management Area in the New Jersey Pinelands. Prescribed burns were conducted on March 22, 2008 and March 15, 2013.

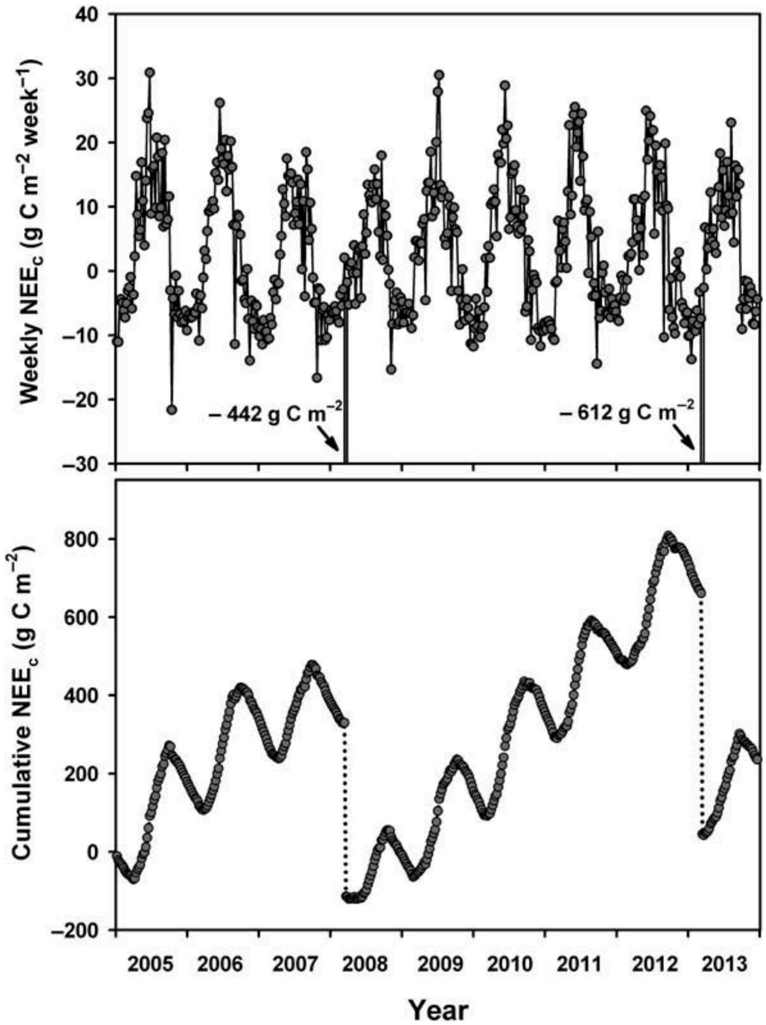

FIGURE 3 Weekly (a) and cumulative (b) net CO_2 exchange (NEE_c, g C m^{-2}) over a 9-yr period at the intensively studied pitch pine-scrub oak stand in Greenwood Wildlife Management Area in the New Jersey Pinelands. Prescribed burns were conducted on March 22, 2008 and March 15, 2013. Consumption of the forest floor and understory vegetation estimated from preburn and postburn biometric measurements is indicated by the arrows.

690 g m^{-2} at 45 yr. In the first 14 yr following prescribed burns, live stem accumulation was also best expressed as a linear function of time since last fire (Figure 4b, Table 3), with an average accumulation rate of 33 ± 3 g m^{-2} yr^{-1}. In contrast, near-maximum amounts of foliage in the understory were achieved within 1 or 2 yr following prescribed burns, and afterward they remained at approximately 100 g m^{-2}. Over the 45-yr chronosequence,

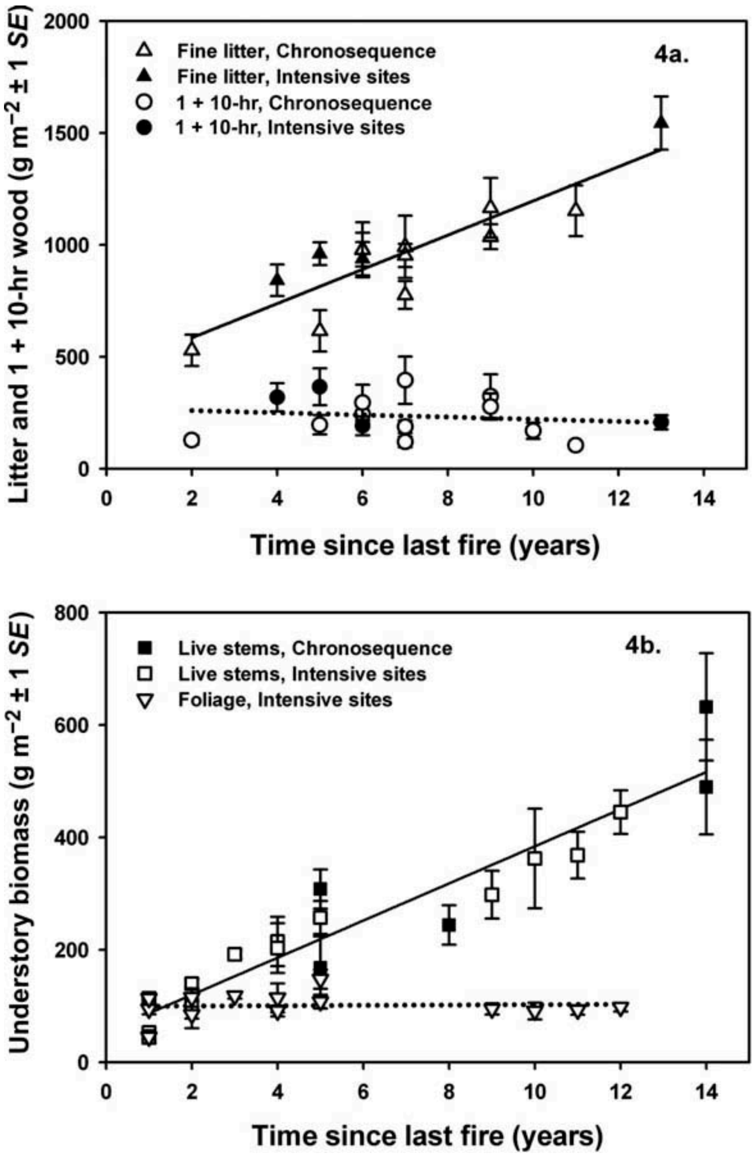

FIGURE 4 Fine litter and woody 1 + 10-hr fuels on the forest floor (a). Shrub foliage and live stem biomass as a function of time since last fire for the 0- to 14-yr time period (b). Slopes of the lines and statistics are presented in Table 3.

accumulation of live stems of shrubs and understory oaks also was best expressed as a power function of time since last fire, with a predicted live stem biomass of 720 ± 332 g m^{-2} at 45 yr. When live + dead stems were considered together, accumulation over the 45-yr chronosequence was best expressed as a linear function of time since last fire (Table 3), with an average accumulation rate of 23 ± 2 g m^{-2} yr^{-1}.

TABLE 3 Summary of Equations Calculated for the Relationships Between Fuel Loading and Years Since Last Fire for 1- and 10-hr Fuels on the Forest Floor, and Foliage and Woody Stems in the Understory

Fuel type	Equation	$\alpha \pm 1$ *SE*	$\beta \pm 1$ *SE*	r^2	*F*	*p*
Forest floor, 0 to 14 yr (Figure 4a)						
Fine litter	Linear	76.4 ± 11.5	431.8 ± 85.8	.77	44.0	< .001
1 + 10-hr wood	Linear	−4.8 ± 8.7	269.2 ± 66.8	.00	0.3	NS
Forest floor, 0 to 45 yr						
Fine litter	Power	666.5 ± 81.0	0.182 ± 0.046	.46	16.9	< .01
1 + 10-hr wood	Power	134.0 ± 70.8	0.291 ± 0.179	.07	2.5	NS
Understory vegetation, 0 to 14 yr (Figure 4b)						
Foliage	Linear	0.3 ± 1.8	99.2 ± 11.1	.00	0.0	NS
Live shrub stems	Linear	33.0 ± 2.8	53.7 ± 21.1	.89	135.9	< .001
Understory vegetation, 0 to 45 yr						
Live shrub stems	Power	113.2 ± 20.0	0.49 ± 0.06	.82	78.2	< .001
Live + dead stems	Linear	23.1 ± 1.6	199.3 ± 32.5	.93	198.5	< .001

Note. Data from the 45-yr chronosequence and the intensively studied tower sites were combined for these analyses. Data were fit to linear equations mass = α * years + β, or power equations mass or live stem biomass = α * (years ^ β).

Forest Carbon Dynamics During Prescribed Fire Intervals

At prescribed fire intervals of 5 to 8 yr (typical values for many of the prescribed burn units managed by NJFFS in the Pinelands), we estimated that net C accumulation by upland forest stands averaged 300 to 840 g C m^{-2} when consumption losses during prescribed burns and accumulation during fire-free periods following burns were considered together. This estimate assumes mean consumption losses of 470 ± 135 g C m^{-2} for the forest floor and understory (Table 1), an annual NEE$_c$ value of 50 g C m^{-2} yr^{-1} for the year of the burn, and an annual NEE$_c$ of 180 g C m^{-2} for each year until the next prescribed burn (Figure 3). For comparison, the intensively studied pine-scrub oak stand accumulated 354 g C m^{-2} over the 5-yr period from March 2008 to March 2013 (Figure 3). Using the predictive equations in Table 3, we estimated that the forest floor would accumulate 172 ± 43 to 275 ± 68 g C m^{-2}, and that live shrub and scrub oak stems would accumulate 103 ± 9 to 149 ± 14 g C m^{-2}, over the 5 to 8 fire-free yr between prescribed burns (Table 3). Carbon accumulation by the forest floor and live stems in the understory at the intensively studied pine-scrub oak stand over the 5-yr period following prescribed burning from March 2008 to March 2013 totaled 218 ± 70 and 139 ± 50 g C m^{-2}, respectively.

DISCUSSION

The carbon dynamics of prescribed burn units in upland forests in the Pinelands is determined by the amount of fuel consumed during prescribed burns; recovery rates of leaf area, respiring biomass and NEE$_c$; and the time until the next prescribed fire, wildfire, or other disturbance. Average consumption and release of C estimated during prescribed fires is equivalent to two to three times the average annual NEE_c in undisturbed but otherwise comparable upland forests (Pan, Birdsey, Hom, McCullough, & Clark, 2006; Scheller et al., 2011; Miao et al., 2011; Clark, Skowronski, Renninger, & Scheller, 2014b). However, net accumulation of C following prescribed burns resulted in C neutrality being achieved within 3 or 4 yr following prescribed burns. Thus, over typical prescribed burn rotations of 5 to 8 fire-free yr, net C accumulation by these upland forests dominated by fire-adapted species was positive and averaged approximately 33 to 58% of NEE_c estimated for undisturbed upland stands.

Although fuel moisture content, prevailing meteorological conditions, and ignition patterns have been shown to be critical factors controlling fuel consumption during prescribed burns (Scott & Burgan, 2005; Ottmar, 2013), our results indicate that initial forest floor and understory biomass are also strongly predictive of consumption during prescribed burns. Specifically, initial biomass explained 75% of the variation in the amounts of fine litter and woody fuel consumed on the forest floor, and 73% of the variation in the amount of understory vegetation consumed. Greater amounts of fine litter but not woody fuels characterized prescribed burn units in pine-dominated stands compared to oak-dominated stands. Differences likely related to litterfall production as well as substrate quality and decomposition dynamics of pine needles versus oak foliage (Gholz, Wedin, Smitherman, Harmon, & Parton, 2000). Higher initial fuel loads in pine-dominated stands resulted in greater amounts of consumption compared to oak-dominated stands. Forest floor and understory biomass estimates reported here are consistent with previous work in the Pinelands, as are the consumption estimates (Burns, 1952; Wright et al., 2007; Clark et al., 2009).

The dominant species in these fire-dependent upland forests in the Pinelands are apparently highly adapted to frequent fires. Specifically, these species appear to have evolved a suite of traits that ensure rapid recovery of leaf area and physiological functioning under the current low intensity but relatively frequent fire return intervals. Ericaceous shrubs and scrub oaks in the understory readily resprout following prescribed fires in the Pinelands (Matlack, Gibson, & Good, 1993), and both pitch and shortleaf pines have epichormic meristems and produce new needle fascicles following disturbance (Little & Somes, 1956). Production of understory and canopy foliage drives C assimilation and NEE_c following prescribed burns. Measurements of leaf-level photosynthetic rates and water use by individual pitch pine trees following prescribed burns in the Pinelands reported by Renninger, Clark, Skowronski, and Schäfer (2013) parallel the rapid recovery of NEE_c that we observed at the intensively studied pine-scrub oak stand. They showed that prescribed burning had either little effect or enhanced photosynthetic rates, productivity, and water use efficiency of overstory pitch pine trees compared to unburned control trees.

Consistent with the results of the current study, we have previously documented highly significant relationships between LAI, evapotranspiration, and NEE_c in upland forests recovering from fire or insect defoliation in the Pinelands (Clark, Skowronski, Gallagher, Renninger, & Schäfer, 2012; Medvigy, Clark, Skowronski, & Schäfer, 2012). In contrast, ecosystem respiration (R_{eco}) is less variable, only slightly reduced immediately following disturbance and then recovering to predisturbance levels by the second growing season (Miao et al., 2011; Renninger, Carlo, Clark, & Schäfer, 2014). Reduced LAI and biomass reduces autotrophic respiration rates as well as the release of soluble C to the rhizosphere, constraining heterotrophic respiration (Clark et al., 2010a). It is also likely that poor litter quality initially constrains decomposition following prescribed burns, and the relative stability of remaining detrital pools limits short-term C loss (Miao et al., 2011). Thus, although LAI is often lower during the first growing season following prescribed burns, R_{eco} also is somewhat reduced, thus daytime NEE_c may be similar preburn and postburn.

Results from the intensively studied pine-scrub oak stand, which was burned twice during the study, indicate that wildland fire managers have some influence over canopy fuel consumption and the recovery of NEE_c in pine-dominated forests. Higher severity prescribed fires or wildfires which result in the consumption of canopy foliage will delay the recovery of leaf area during the next growing season. Reduced LAI results in lower rates of C assimilation and NEE_c during the growing season compared to preburn periods and lengthens the time to achieve C neutrality. By controlling prescribed burn intensity and the amount of crown scorch through the choice of firing techniques and ignition patterns, as well selecting days with desired fuel moisture contents, wind and RH conditions during the prescribed burn, fire managers have the ability to "fine-tune" prescribed fires to maximize hazardous fuel reduction while minimizing crown scorch and canopy consumption.

The patterns of recovery of the litter layer, understory vegetation, and NEE_c measured in the Pinelands are consistent with those reported from other fire-dependent pine-dominated ecosystems where similar measurements have been made before and following prescribed burns. For example, at a slash pine (*P. elliotii* Engelm.) and longleaf pine (*P. palustris* Mill.) stand near Gainesville, Florida, USA, a prescribed burn conducted in January 2003 consumed 94 and 73% of the litter layer and understory, respectively. Litter layer and understory vegetation C had recovered to 45 and 53% of preburn biomass within 1 yr of the prescribed burn, and NEE_c and soil CO_2 fluxes during the following growing season were close to preburn levels (Powell et al., 2008; Lavoie, Starr, Mack, Martin, & Gholz, 2010; Godwin, 2012). Whelan, Mitchell, Staudhammer, and Starr (2013) observed that daytime NEE_c in mesic, intermediate, and xeric longleaf pine stands recovered to preburn levels within 2 months of prescribed burns. However, annual NEE_c values indicated that only the mesic stand sequestered C, while the intermediate and xeric stands lost C. It is notable that extreme drought affected NEE_c rates in all three stands in the years following the prescribed burns reported by Whelan et al. (2013).

Over longer time periods and multiple prescribed burn intervals, simulations based on consumption data reported here, as well as NEE_c measurements made at the intensively studied pine scrub oak stand and two other carbon flux towers in the Pinelands (Clark et al., 2010a), indicate that fuel-reduction treatments may have only minor effects on long-term forest C dynamics. Scheller et al. (2011) used LANDIS-II model coupled with CENTURY and the Dynamic Fire and Biomass Fuels extensions to simulate current management practices, including prescribed burning and wildfire suppression as reflected by recent (1991–2006) fire records, over a 100-yr period in the Pinelands. In a second set of simulations, they increased the area treated by prescribed burning by approximately 50% over current acreage burned. Both sets of model simulations suggested that upland forests in the Pinelands would continue to sequester C over the next 100 yr under current climatic conditions. Although aboveground net primary production, live biomass, and forest floor C were predicted to be nearly constant or increased only modestly, soil organic C continued to increase slowly through time in all forest types except the most frequently burned pitch pine-scrub oak stands, consistent with the observations of Neill et al. (2007) and Williams et al. (2012). Therefore, current and modest increases in prescribed burning practices in upland forests are predicted to have only minor effects on landscape scale forest C dynamics in the Pinelands over longer time scales.

CONCLUSIONS

Fine litter and understory biomass were greater in pine-dominated than in oak-dominated prescribed burn units, but 1-hr and 10-hr woody fuels were similar among upland forest communities. Consumption of forest floor and understory vegetation were significant linear functions of initial mass, accounting for 75% and 73% of the variation in amounts consumed during prescribed fires, respectively. Consumption averaged 470 ± 135 g C m^{-2} across all three upland forest communities and was equivalent to 2- to 3-yr NEE_c in undisturbed upland stands. Recovery of leaf area and NEE_c following prescribed burns was rapid, with understory LAI approaching preburn levels by the end of the growing season of the year of the burn, while recovery of canopy LAI in pine-dominated stands was dependent upon prescribed burn intensity. Daytime NEE_c approached preburn levels during the growing season of the year of the burn, and it had recovered completely by the next year following prescribed burns. During typical rotation intervals of 5 to 8 fire-free yr between prescribed burns employed by the NJFFS, prescribed burn units were estimated to have accumulated 300 to 840 g C m^{-2}, approximately 33 to 58% of estimated C accumulation in undisturbed upland forest stands over the same time period.

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